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Lichen–Invertebrate Associations

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I. Introduction

Interest in lichen invertebrates has been flickering for many years, fanned mostly by individual botanists and zoologists often not conversant with the complementary discipline. Soil zoologists (i.e. Kühnelt, 1976; Stebaev, 1963) have contributed their observations, as well as naturalists (Cunningham, 1907), marine biologists (Colman, 1939) and many others. Smith (1921) was the first to sum up and review such associations, devoting a section in her book to lichens as food and shelter for invertebrates. More recent efforts, stimulated by interest in population dynamics (Broadhead, 1958), mite and nematode ecology (Travé, 1963; Gadea, 1974) and beetle taxonomy (Gressitt, 1966), among others, have materially contributed to this still largely unknown field. The effect of industrial air pollution on lichen communities has also focused interest on the resultant changes in distribution of moth (and other insect) morphs (Kettlewell, 1961, 1973). Although interest in the subject is rising, as evinced by the steady publication of lichen–invertebrate papers in the *Lichenologist*, a strictly botanical periodical, such recognition is by no means universal.

The present chapter developed from the senior author's review of arthropods associated with lichens (Gerson, 1973); some subjects treated there will not be repeated here. It must be emphasized that most data were gleaned from a variety of botanical, zoological and ecological publications, and some care must therefore be exercised in applying scientific names.

Travé (1963) made the pertinent observation that there are actually two more or less mutually exclusive faunas on lichens (and mosses): an aquatic fauna and a terrestrial one. Protozoa, Nematoda, Rotifera and Tardigrada belong to the former, whereas Arthropoda and Mollusca belong to the latter. Some overlap between the two faunas exists, and invertebrates living on marine lichens are ignored by this division. Nevertheless, despite certain reservations, it is a very convenient concept and has been adopted here.

II. The Aquatic Fauna

A. Protozoa

Almost all humid habitats harbour protozoans. However, only a few protozoans are actually associated with specific plant taxa; examples are the ciliate *Zoothamnium adamsi* which forms colonies on the alga *Cladophora*, and the flagellate *Phytomonas*, living in the sap of *Euphorbia*. No protozoans are known to be specific to lichens.

Only two of the four major divisions of the Protozoa, namely the rhizopods and ciliates, have been found in association with lichens. Of the former group, the most abundant appear to be the testate or shell-bearing normally (100–150 µm) amoebae, usually known as thecamoebae (which are also the commonest soil protozoans). Several European workers, Decloitre (1962), Gadea (1964a), Heinis (1959) and Laminger (1971), collected lichen thecamoebae from Norway, the Spanish Mediterranean coast and the Alps, respectively. The genera commonly collected were *Archella*, *Centropyxis*, *Euglypha* and *Trinema*. Decloitre (1962) and Laminger (1971) listed the protozoans they collected according to lichen habitat, but no pattern emerges from a perusal of their lists. Species found exclusively in saxicolous lichens by one of these investigators occurs only in terrestrial lichens according to the other. The abundance and diversity of thecamoebae found suggest further research possibilities.

Quantitative data are limited; Laminger (1971) found the terrestrial *Cladonia stellaris* to be richest in thecamoeban numbers, but this may include soil populations. Heinis (1959) stated that pure lichen stands usually have a poor fauna, an opinion shared by Gadea (1964a). Such a poor fauna possibly reflects not only a certain unsuitability of lichens for components of the microfauna, but also, and perhaps more importantly, an early phase in soil and humus formation. As to relative abundance, Gadea (1964b) estimates that thecamoebae account for 27% of the lichen microfauna.

Most free-living protozoans endure dry periods by forming cysts, a state in which they may survive for long periods. Cysts are blown about by wind, and are thus widely transported. Alternatively they may remain on the lichen until it is rewetted; Heinis (1959) found thecamoebans on Mt Macun (2620 m), in the eastern Swiss Alps, in dry thalli of *Cladonia*, *Parmelia* and *Lecanora*.

Among ciliates, the genus most often collected in lichens is the kidney-shaped holotrichid *Colpoda* (Gadea, 1964a, 1974; Thompson, 1960). Members of this genus are common in fresh water, soils and some land slugs, and have a most efficient encystment mechanism (Stout and Heal, 1967).

Members of a third major protozoan division, namely the flagellates, are probably associated with lichens in an indirect way—through being symbiotic in reindeer rumen, and there participating in the digestion of lichens (Scotter, 1965).

B. Nematoda

The nematodes or roundworms are abundant in marine and fresh water, in soil, dung, and as plant and animal parasites. The terrestrial forms are usually small (<1 mm), thin worms which require some water for their activities. Gadea (1964a, b, 1973, 1974) did not find any lichen-specific species; the phytophagous ones are all bryophagous. In his latest report he compared the nematode faunas associated with three lichen species (Table I). It is noteworthy that these faunas, collected from different Mediterranean regions, are actually quite similar, despite variable dominance by different species. Gadea (1964b) concluded that nematodes comprise a substantial part (29%) of the lichen aquafauna.

TABLE I

Relative abundance of lichen-associated nematodes (from Gadea, 1974).

Nematodes	*Cladonia foliacea* (%)	*Xanthoria aureola* (%)	*Xanthoria parietina* (%)
Aphelenchoides parietinus	6	2	4
Ditylenchus intermedius	–	33	6
Ditylenchus sp	18	–	–
Eudorylaimus carteri	–	–	14
Mesodorylaimus bastiani	–	6	–
Panagrolaimus rigidus	–	12	7
Plectus cirratus	20	26	55
Rhabdolaimus terrestris	–	5	–
Tylenchus filiformis	56	16	14

Few additional reports on lichen nematodes are available. Goodey (1933) noted some species, especially the Araeolaimids *Plectus* and *Wilsonema* (the former, which also figures in Gadea's lists, from house roof lichens). Ali *et al.* (1970 and other papers) have reported on Indian lichen nematodes.

Nematodes survive dry periods by forming resistant resting stages and by encystment. Nielsen (1967), in a study on roof moss-inhabiting nematodes, noted that some species, like *Plectus cirratus*, *Tylenchus filiformis* and *T. davainei*, which also occur in lichens, are quite resistant to desiccation.

C. *Rotifera*

The Rotifera or Rotatoria (also called "wheel animalcules") are common in freshwater or marine benthic habitats, some species being parasitic on animals, and others living on mosses and lichens. Heinis (1959 and former publications), in his studies on cryptogam "Mikrocoenoses", reported on many rotifers in lichens. Pure stands of *Solorina crocea* harboured *Adineta barbata* and *Ceratrocha cornigera*, and *Macrotrachela ehrenbergii*, *Pleureta alpina* and *Mniobia* spp. were found in dry thalli of *Cladonia pyxidata* and *Parmelia* spp. Gadea (1964b, 1974) collected *Callidina* from *Xanthoria aureola* and some philodines from other lichens, and estimated that rotifers account for about 8·5% of the lichen aquatic microfauna.

Feeding on lichen ascospores by rotifers was described by Pyatt (1968), who obtained *Philodina* from apothecial surfaces of *Xanthoria parietina* and reported that some ascospore breakdown occurred within the rotifer's body, especially when only a few (3–8) ascospores were ingested.

D. *Oligochaeta*

The Oligochaeta are represented in the lichen fauna only by members of the family Enchytraeidae. Colman (1939) collected specimens of *Lumbricillus* in *Lichina pygmaea* tufts off the British coast, calculating that there were about 220 individuals per m^2 of rock. Frankland (1974) cited P. M. Latter as rearing enchytraeids on *Cladonia*, as the only source of food.

E. *Tardigrada*

Tardigrades or "bear animalcules" are small, eight-legged invertebrates which occur in damp soils, on various cryptogams and in both marine and freshwater habitats. They feed on debris and moss cells, and a few are predacious (Cuénot, 1949; Marcus, 1959). Tardigrades are capable of withstanding long dry periods by forming cysts or by anabiosis. Anabiosing animals (tuns) and tardigrade eggs are widely disseminated by winds, often along with small lichen propagules (Cuénot, 1949). No clear reports on lichenophagous tardigrades could be found, but as bryophagous species are frequently collected in pure lichen stands, such feeding habits may be assumed. Argue (1971), Iharos (1968) and Schuster and Grigarick (1966), among others, found tardigrades in various lichens in Canada, Mongolia and the Galápagos Islands, respectively. Argue (1971) reported *Hypsibius oberhaeuseri* and *Pseudechiniscus suillus* only on *Lobaria pulmonaria*, although some mosses were also sampled. The former tardigrade is quite common in lichens, being especially abundant on *Xanthoria* thalli (Cuénot, 1949). Schuster and Grigarick (1966) obtained various tardigrades from *Parmelia*, *Cladonia* and *Ramalina* including the cosmopolitan *Macrobiotus hufelandii* and *Milnesium tardigradum* which occur on many lichens (Heinis, 1959; Marcus, 1959).

Kimmel and Meglitsch (1969) found lichen-inhabiting tardigrades on lichen-covered, and not lichen-free, tree bark in Iowa, suggesting that this substrate is required. Their data indicate some lichen preference among the tardigrades obtained: *M. tardigradum* occurred most often in *Candelaria concolor* and *Physcia millegrana*, and *Hypsibius tuberculatus* preferred *Arthonia caesia*. Furthermore they showed that some tree-lichen combinations were more suitable for tardigrades than others, and that the population density of these animals changes according to the height of the corticolous lichen above ground level.

Barrett and Kimmel (1972) reported that tardigrade density and diversity within colonies of bark-colonizing *Physcia* were much reduced following DDT treatments. They concluded that tardigrade species occupy contiguous, non-overlapping niches within the lichen-bearing tree (*Ulmus*) bark ecosystem. The use of such simple ecosystems was advocated by Barret and Kimmel for evaluating the effects of pesticide stress on forest ecosystems, and for energy flow and mineral recycling studies.

From the limited data available, it would appear that tardigrades are a minor component of the Mediterranean lichen fauna; Gadea (1964b) stated that they accounted for only about 0·5% of the lichen microfauna which he studied.

III. The Terrestrial Fauna

Insects, mites and molluscs constitute important components of the terrestrial fauna and are the main lichen grazers. Although these animals are grouped within the terrestrial fauna (Travé, 1963), many species become active only when the lichen is wet. Marine molluscs, like the periwinkles, are discussed here only for taxonomic convenience. Travé's contention that the two faunas are mutually exclusive would appear to require some modification.

A. Insecta

Insects are the largest class in the animal kingdom, and are proportionally represented in the lichen-associated fauna. Examples of the wingless insects—subclass Apterygota—come from the Thysanura (bristletails), the Collembola (springtails) and the Protura. The latter sometimes occur in lichens (Nosek, 1973). Kühnelt (1976) writes that the thysanuran Machilidae feed mainly on lichens and algae, and Benedetti (1973) reports that the food of *Neomachilis halophila*, a Californian bristletail, contains unicellular algae which were derived from a rock-encrusting lichen under which it lives. A few individuals of *Petrobius* and *Lipura*, other machilids, were found in *Lichina pygmaea* tufts by Colman (1939).

Some springtails feed on lichens (Kühnelt, 1976). Hale (1972) described the feeding of *Hypogastrura packardi* on the corticolous *Parmelia baltimorensis*, noting that the upper cortex and most of the algal layer were completely eaten away. Thousands of collembolans were seen there, causing large areas in the central part of the lichen to disintegrate and fall away. This grazer was estimated to reduce the lichen colony by at least 50%. A xerophilic fauna was found by Hale (1963) in lichens of an eroding blanket bog in England. The lichen colony of *Cladonia* spp. developed on a hag lip, a relatively dry area in such bogs, and harboured large numbers of collembolans. Heavy infestations of collembolans can almost obliterate the crustose lichens beneath: such observations have been made by M. R. D. Seaward (unpublished data) for the collembolan *Hypogastrura tullbergi* on various crustose lichens on saxicolous substrates, and for *Anurophorus laricis* on epiphytic *Pertusaria pertusa* (Seaward, 1975). Byazrov *et al.* (1976) provide data on collembolan species composition of lichen synusia in Mongolia, and Ridley (1930) mentions the possible dispersal of *Pertusaria amara* by springtails.

The Pterygota—winged or secondarily wingless insects—are divided into those with simple metamorphosis, the Exopterygota (or Hemimetabola), and those with complete metamorphosis, the Endopterygota (or Holometabola). Representatives of eight exopterygote orders have been recorded from lichens. The best known examples are the Psocoptera (psocids or barklice), voracious lichen feeders (Seaward, 1965; Laundon, 1971) whose feeding preferences were extensively studied by Broadhead (1958).

In northern England, the psocids living on larch trees (*Larix decidua*) comprise two distinct feeding groups. Six of the eight commonest psocid species feed primarily on the *Desmococcus*-fungal spore mixture occurring on the bark of the twigs and branches. These species are: *Mesopsocus immunis*, *M. unipunctatus*, *Philotarsus picicornis*, *Amphigerontia bifasciata*, *Elipsocus westwoodi* and *E. hyalinus*. None of these species appears to discriminate between *Desmococcus* and fungal spores. When the preferred foods are scarce, these species will take some lichen, but lichen is an unsatisfactory food for them, producing higher mortality rates and lower oviposition rates. The remaining two species, *Elipsocus mclachlani* and *Reuterella helvimacula*, feed primarily on the lichen *Lecanora conizaeoides*, which is the predominant lichen species on larch in northern England. When this lichen is scarce or absent, these lichen-preferring species will nevertheless readily accept *Desmococcus* and fungal spores on which they thrive in the laboratory. The various food components (*Desmococcus*, the spores of honeydew moulds, lichen, bark flakes and structureless detritus) can be identified in the crops of these insects and their relative abundance estimated. Quantitative comparisons of the crop contents of these psocid species have been set out by Broadhead (1958, his Table 4). Photographs of crop contents to show some of these food components are presented in Fig. 1.

Representatives of the Orthoptera often mimic lichens: katydids (Tettigoniidae), grasshoppers and stick insects (Phasmida) include some bizarre lichen-like forms (Chopard, 1938; Cott, 1957). A colour photograph of a Congolese lichen mantid was presented by Farb (1963). Feeding on lichens by grasshoppers was reported by Richardson (1975) from American sources.

The webspinners or Embioptera are little-known insects which construct silken tunnels in which they live. Ross (1966) described a sea-shore habitat in the Galápagos Islands where epiphytic and saxicolous lichens are covered by the silk of *Chelicerca galapagensis*, which apparently feeds on the lichens. A lichen-feeding embiid was also recorded from Australia (Anon., 1970).

Less information is available concerning the relationships of other exopterygote orders with lichens. Some, like the stoneflies (Plecoptera) and the termites (Isoptera), rarely feed on lichens (Coleman and Hynes, 1970; Kalshoven, 1958). Thrips (Thysanoptera) sometimes hide in lichens (Dev, 1964; Kühnelt, 1976). Earwigs (Dermaptera) participated in the lichen-feeding experiments summed up by Smith (1921), and several British bugs (Hemiptera) were listed from lichens by Southwood and Leston (1959). Among these is *Loricula elegantula*, a predacious bug closely associated with *Parmelia*, which feeds on barklice, including *Reuterella helvimacula*, a known lichen feeder (Broadhead, 1958).

Among the holometabolous insects, the butterflies and moths (order Lepidoptera) have evolved the richest associations with lichens. Many feed on these plants (Brightman, 1965; Anon., 1970; Borror and DeLong, 1971), cover their cases with lichen fragments (Weber, 1974), or mimic them (Cott, 1957). Members of the moth family (or subfamily) Lithosiidae

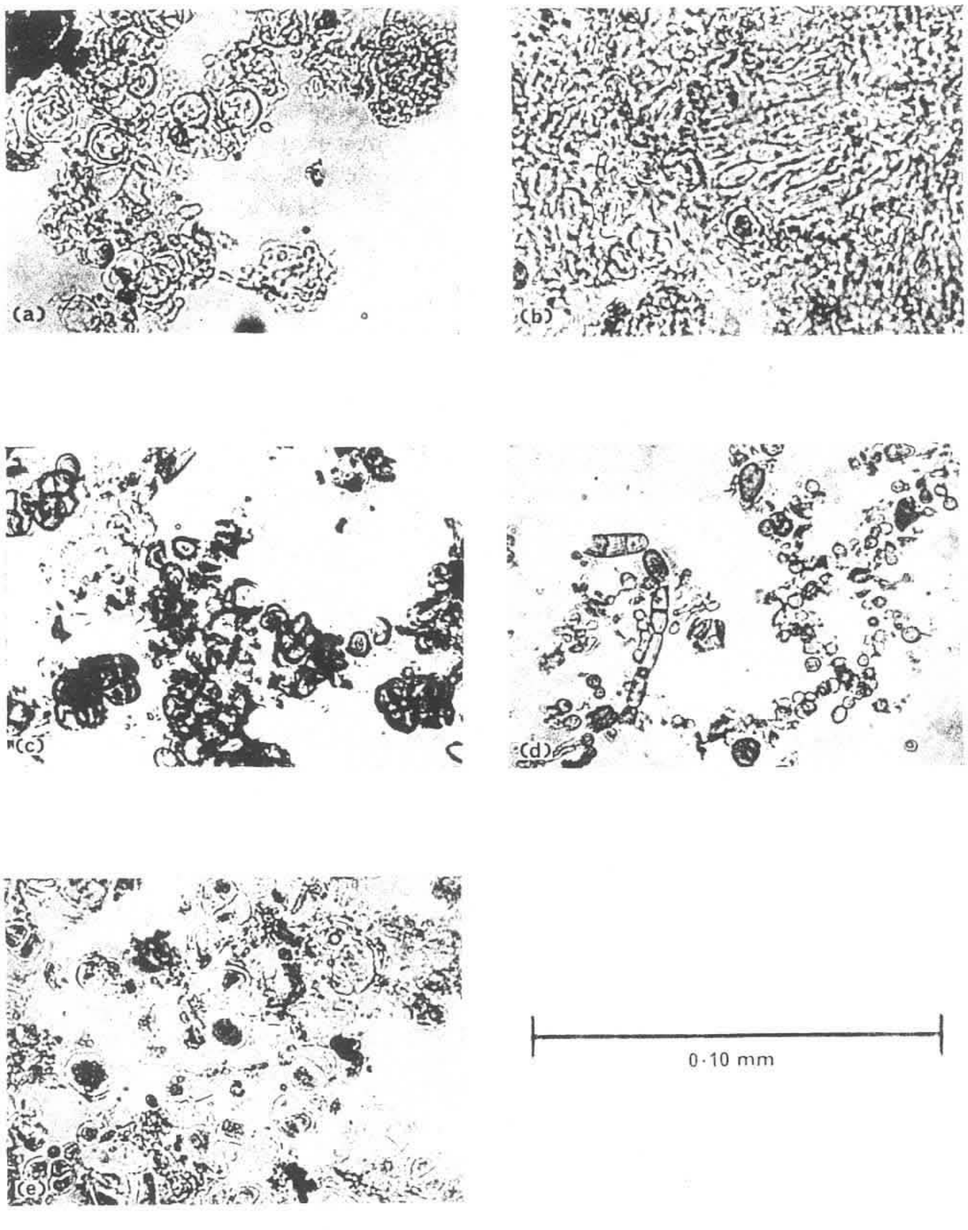

FIG. 1. Portions of the crop contents of various larch-living Psocoptera to show the chief food components: (a) lichen algal cells and hyphae (*Lecanora conizaeoides*) from *Reuterella helvimacula*; (b) lichen hymenium (*Lecanora conizaeoides*) with ascospores from *Elipsocus mclachlani*; (c) the honeydew mould *Sporidesmium* from *Amphigerontia bifasciata*; (d) small fungal spores and hyphae from *Elipsocus westwoodi*; (e) *Desmococcus* from *E. westwoodi* (E. Broadhead, unpublished data).

live in, feed on, and mimic lichens (Richardson, 1975). Their close association has resulted in various appropriate vernacular names (Table II). According to Mani (1962), some Lepidoptera belong to the communities of "yellow, orange and red" saxicolous high-altitude lichens, thus contributing to the developing, colonizing lichen fauna. Caterpillars of the subfamily Meessiinae (Tineidae—clothes moths) are believed to be lichenophagous; they carry cases which imitate their substrate and in which they pupate (Zagulyayev, 1970). Some caterpillars appear to "thrive" on mosses and lichens (de Boer, 1975). Breakdown of the lichen-mimicking protective crypsis of moths on soot-discoloured walls and tree trunks has often been discussed within the context of industrial melanism (Kettlewell, 1961, 1973).

TABLE II

Lichen-associated moths of the family Lithosiidae (Lepidoptera), and their vernacular names (compiled from Holland, 1908).

Moth	Vernacular name
Crambidia pallida	Pale lichen moth
C. casta	Pearly-winged lichen moth
C. allegheniensis	Alleghenian lichen moth
Hypoprepia miniata	Scarlet-winged lichen moth
H. fucosa	Painted lichen moth
Haematomis mexicana	Mexican lichen moth
Comacla simplex	Mouse-coloured lichen moth
Bruceia pulverina	Powdered lichen moth
Clemensia albata	Little white lichen moth
Illice unifascia	Banded lichen moth
I. subjecta	Subject lichen moth
I. nexa	Yellow-blotched lichen moth
Ptychoglene phrada	Druce's lichen moth
P. tenuimargo	Narrow-banded lichen moth
Pygoctenucha funerea	Funereal lichen moth
P. terminalis	Blue-green lichen moth
Lerina incarnata	Crimson-bodied lichen moth

Beetles (order Coleoptera) also have diverse associations with lichens, but they appear to have been less studied. The fungus weevil *Lichenobius littoralis* lives and excavates tunnels in *Pertusaria graphica* (Holloway, 1970). An elm-leaf beetle was reported by Smith (1921) to resemble apothecia of *Physcia*, and Gressitt (1966) presented photographs of New

Guinea weevils whose dorsum was extensively overgrown with *Parmelia*. These weevils are believed to have evolved special depressions and exudations on their dorsum which facilitate and promote the growth of the cryptogams. Dermestid beetles were obtained from *Parmelia centrifuga* stands in the South Ural Mountains by Stebaev (1963).

Lacewings (order Neuroptera) are predacious insects whose larvae sometimes cover themselves with lichen "packets" (Garrett, 1974; Skorepa and Sharp, 1971). This habit, which probably evolved as camouflage, also serves to disperse soredia when the moulting larvae leave their old, lichen-covered skins behind.

Very little has been reported on the associations of the two remaining orders, Diptera and Hymenoptera, with lichens. Stebaev (1963) obtained up to 135 dipterans (members of the families Empididae and Cecidomyiidae) per dm^2 of *Parmelia*. Séguy (1950) noted gall midges (family Cecidomyiidae) as they were developing in mosses and lichens. Richardson (1975) reported on sciarid larvae which feed on lichens, and Bullock (1966) working in Singapore, noted a dipteran which closely resembles the sporulating bodies of lichens. Concerning Hymenoptera, ants have been found in association with lichens: Béique and Francoeur (1966) collected various Canadian ants from nests which were built underneath *Cladonia* stands, and Bailey (1970) described the dispersal of *Lecanora* soredia by ants. Some unidentified dipterans and hymenopterans were found by Bengtson *et al.* (1974) in Spitsbergen lichen stands.

To conclude, representatives of 15 (i.e. more than half) of the insect orders associate with lichens in one way or another, and further studies will no doubt reveal even more. It is appropriate to conclude this section with the picturesque account given by Cunningham (1907, p. 151):

> The originally smooth surfaces which are left on the stems of many palm-trees by the fall of successive crops of leaves are usually quickly clothed in a coating of crustaceous lichens, painted on in intricate patterns of softly blended colours, and forming a pasture ground on which many different sorts of small insects browse happily.

B. Mites (Acari)

Evans *et al.* (1961) recognized seven orders within the Acari, a classification which, although not universally accepted, is followed here. Four of these orders, namely the Cryptostigmata, the Prostigmata, the Astigmata and the Mesostigmata, have been reported from lichens. A list of Acari collected in the orange lichen intertidal zone in Britain was compiled by Evans *et al.* (1961).

The Cryptostigmata (Oribatei, beetle or moss mites), dark, slow-moving Acari, often graze on or burrow within lichen thalli. Some, like *Pirnodus detectidens*, occur mostly in saxicolous lichens, whereas others, for example *Dometorina plantivaga*, prefer corticolous species; both of these feed exclusively on lichens (Travé, 1963, 1969). Others, like *Oribatula parisi*, are found in mosses as well as lichens. Only immature specimens of *Mycobates parmeliae* live in lichens, the adults being more abundant in mosses and hepatics. Other lichen-frequenting cryptostigmatids, like *Phauloppia lucorum*, appear to be non-specific feeders (Travé, 1963; Seaward, 1974).

Camisia segnis deposits its eggs in lichens. During oviposition some softening substance is excreted by the female which causes the lichen to swell and grow over the egg, thus protecting it (Grandjean, 1950). As the egg hatches, the emerging larva feeds, moults and continues to develop there. Another cryptostigmatid, *Ommatocepheus ocellatus* (Fig. 2) also feeds within the thallus; its periods of activity are correlated with the humidity of the host-lichen. The nymphs (Fig. 2) possess large leaf-like dorsal setae, which probably serve to protect them from desiccation (Travé, 1963). Similar observations are reported for *Dometorina plantivaga* and *Pirnodus detectidens* (Travé, 1969). More than a dozen additional cryptostigmatids associated with lichens were listed by Travé (1963), and numerous other associations are noted by Seyd (1968 and former publications).

Information about lichen-feeding Prostigmata is much rarer. *Tydeus tilbrooki*, possibly the smallest free-living arthropod in Antarctica, feeds on fungal hyphae and lichens (Strong, 1967), and occurs as very dense populations within *Ramalina* and *Caloplaca* thalli (Gressitt and Shoup, 1967). *Tydeus tilbrooki* deposits its eggs on the lichen, where they look like pale-pink spots. Another tydeid, *Paralorryia mali*, includes lichens in its diet (Gerson, 1968). Coineau (1973) found the caeculid *Microcaeculus hispanicus* in rock-encrusting stands of *Parmelia stenophylla* and the moss *Grimmia campestris*. Additional species, representing diverse families, are suspected of being lichen feeders. They include *Cryptognathus lagena*, found on a saxicolous *Parmelia*, whose food may have been extracted from the thallus (Luxton, 1972), *Ledermuelleria* spp., known to feed on mosses (Gerson, 1972) but also collected in lichens, and *Daidalotarsonemus* spp., whose greenish bodies and lichen habitat lend support to the above theory (Gerson, 1971). Representatives of several other prostigmatic families were obtained in sparse numbers from Belgian corticolous lichens by Andre (1975). Prostigmatids found in sea-shore lichens are listed by Evans *et al.* (1961).

"*Tetranychus lápidus*" is a name which has persistently been listed

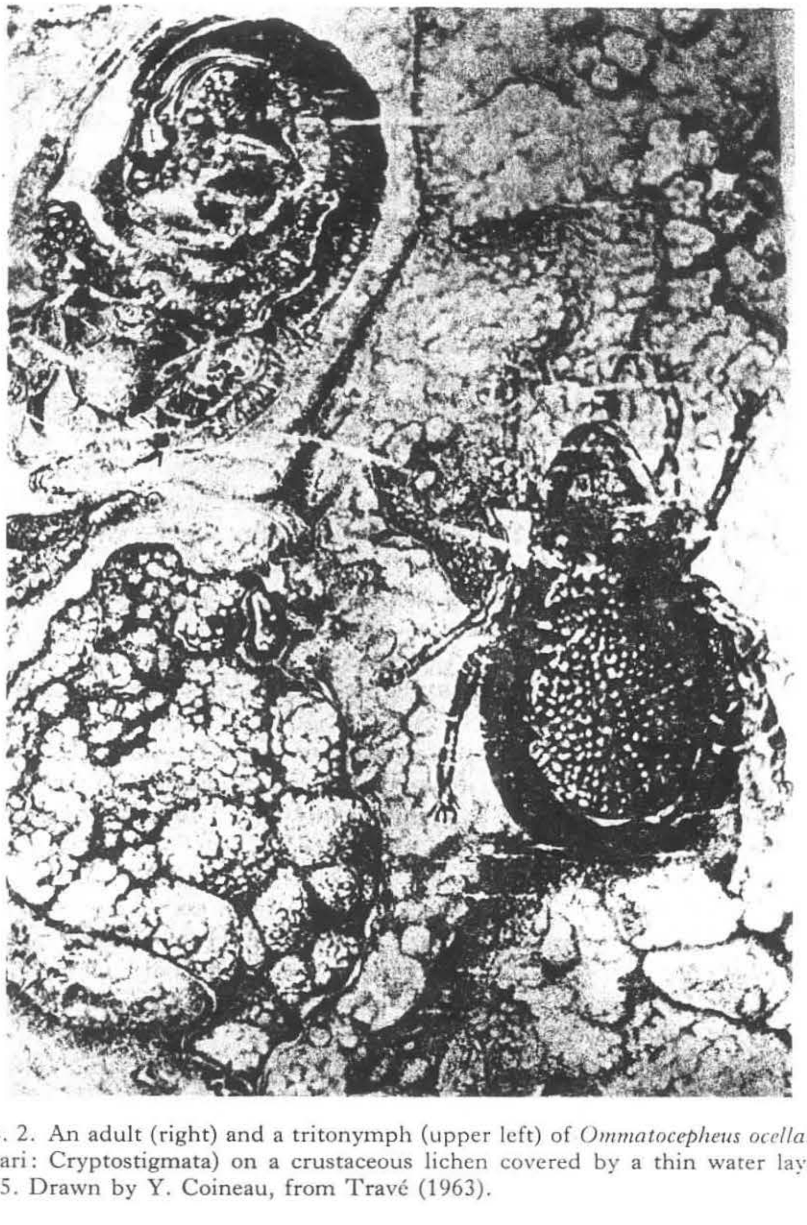

FIG. 2. An adult (right) and a tritonymph (upper left) of *Ommatocepheus ocellatus* (Acari: Cryptostigmata) on a crustaceous lichen covered by a thin water layer ×95. Drawn by Y. Coineau, from Travé (1963).

among the lichen mites (Wheldon, 1914; Smith, 1921; Richardson, 1975). This mite is actually *Petrobia latens*, the brown wheat mite, a member of the prostigmatic family Tetranychidae. It is a pest of many low-growing monocotyledonous plants in the southwestern United States, being known also from Europe, North Africa and Australia (Baker and Pritchard, 1953). *P. latens* deposits its characteristic, whitish, saucer-like diapause egg, with its radially-striated cap, on and under stones and stray bits of wood, their presence on lichens probably being fortuitous. There are no published records of actual lichen-feeding by this mite. Wheldon (1914), who first associated "*Tetranychus lapidus*" with lichens, cautiously wrote that "It is possible that the Acari feed upon these plants", but presented no further proof. Wheldon also noted that "on crushing [the eggs] they exude a thin reddish fluid". This observation was later the basis of the "blood from a stone" hoax entertainingly related by Browning (1950).

Gall mites (Eriophyoidea, tentatively retained in the Prostigmata) form galls on lichens—and lichens are the only Thallophyta on which Acari form galls (Mani, 1964).

Several astigmatids, referable to the families Saproglyphidae and Hyadesidae, were found in lichens colonizing subantarctic islands (Hughes and Tilbrook, 1966; Fain, 1975). At least one of these mites, *Hyadesia halophila*, belongs to a phytophagous genus whose members feed on algae; some lichen feeding may also take place. Unidentified Astigmata were collected by Andre (1975) from corticolous *Lecanora conizaeoides* in Belgium.

The role of mesostigmatic mites in lichen communities is obscure. Some predacious species were listed from British shore lichens by Evans *et al.* (1961). Travé (1963) stated that members of the family Epicriidae are present in dense lichen stands, Tilbrook (1967) recorded several specimens of *Cyrtolaelaps racovitzai* from lichens in maritime Antarctica, and Stebaev (1963) found *Zercon* in South Uralian *Parmelia* material. The association of these mites with lichens is probably quite casual. On the other hand, the occurrence of many predacious Phytoseiidae in Belgian corticolous lichens (Andre, 1975) suggests that they may play some role in that ecosystem.

C. Other Arthropods

Various additional terrestrial and aquatic arthropods are associated with lichens. Among the predacious Arachnida, spiders (Araneae), such as the South American *Azilia*, disguise their snares with bits of lichen, which harmonize with the spider's colours (Cott, 1957), and the giant crab spider from Trinidad (Cooke, *in litt.*) constructs its nest from lichens (mainly

Usnea). Other spiders are to be found in tundra lichens (Bengtson *et al.*, 1974). Pseudoscorpions (Chelonethi) hunt for lichen-grazing barklice in the Chaco region (Morello, 1970). The opilionid (Phalangida, harvestmen) *Phalangium opilio* has an irregular light and dark colour pattern, which makes it rather unlike a phalangid, while blending with a lichen-covered background (Cott, 1957). Unidentified "Myriapoda" were obtained by Stebaev (1963) from *Parmelia centrifuga* in the South Ural Mountains, and the diplopod *Polyxenus* was found in galls of *Ramalina kullensis* collected in Sweden (Zopf, 1907).

Crustaceans settle on, live in, feed upon and compete with lichens in marine environments. Barnacle (Cirripedia) spat may settle on littoral lichens, but very few stay for longer than two weeks, probably due to an imperfect adhesion to some plant surfaces (Fletcher, 1973). Moderate numbers of *Chthamalus stellatus* and *Balanus balanoides* were found amongst *Lichina* tufts (Colman, 1939). Competition for settling sites between lichens and barnacles was described by Fletcher (1973); once established, lichens appear to resist additional colonization by the cirripedes. A scheme of the rocky-shore barnacle-and-lichen zone was presented by Stephenson and Stephenson (1972).

Wieser (1963) studied relationships between *Lichina pygmaea* and the crustacean isopod *Campecopea hirsuta*. This isopod feeds on the lichen by browsing along its branches, eating away the gonidial layer and leaving the mycobiont almost undisturbed. *L. pygmaea* is the isopod's preferred habitat, and Colman (1939) found several thousand specimens in the small tufts of this lichen. *Campecopea* feeds only when its habitat is wet, being, in this respect, like members of the aquafauna. Like them, it is also very resistant to desiccation (Wieser, 1963), another feature amply demonstrated by components of the lichen-associated fauna. Colman (1939) also recorded the amphipod *Hyale nilssoni* in *L. pygmaea* tufts, but its occurrence is probably fortuitous.

D. Mollusca

Representatives of two of the major classes of the Mollusca, namely the Gastropoda and the Bivalvia, associate with lichens. The gastropods—snails, slugs and periwinkles—are terrestrial or intertidal in habit. *Lasaea*, the best-known lichen-associated bivalve, is marine.

Snails feed on lichens (Plitt, 1934; Peake and James, 1967; Coker, 1967), shelter within their stands and disperse their propagules. Shore lichens, like *Arthopyrenia* and *Verrucaria*, settle on living or dead mollusc shells. These associations were reviewed by Peake and James (1967), who also listed British snails and slugs observed with lichens. Holden and Tracey (1950) noted the presence of enzymes which break down the common lichen polysaccharide lichenin in the alimentary tract of snails, and Nielsen (1963) found laminarinase (=lichenase) in the slug *Arion*.

Several species of the periwinkle *Littorina* occur in maritime *Verrucaria* spp. These gastropods are the only conspicuous animals in the middle and lower *Verrucaria* belts in the British Isles (Stephenson and Stephenson, 1972), and are also common on tufts of *Lichina pygmaea* (Colman, 1939). Limpets (*Patella* spp.) graze on littoral lichens in the British Isles, and may even limit the cryptogams' initial colonization, although they avoid firmly established colonies (Fletcher, 1973).

The bivalves *Mytilus edulis* and *Lasaea rubra* both occur on *Lichina*, the former in scant numbers, the latter in large populations (Colman, 1939). *L. rubra* has the remarkable ability to recover from a 12-h exposure to 30°C and dry air. This capability is even more pronounced in *Lasaea*—an obvious adaptation to living in lichens which may dehydrate during midday low tides (Morton *et al.*, 1957). Such a mechanism is reminiscent of the various adaptations to desiccation developed by members of the lichen aquafauna and suggests a degree of eco-physiological convergence. Colman (1939) sampled several species of algae as well as *Lichina* for invertebrates, but *Lasaea* was recovered only from the lichen. Some specific, non-trophic association is thus indicated as *Lasaea*, like other bivalves, is a ciliary feeder and does not use *Lichina* as food. The nature of the association between the bivalve and the lichen remains an open question.

IV. Distribution

A. Habitats

Invertebrates associate with lichens wherever they grow: in primitive soils (Richardson, 1975), on rocks undergoing weathering (Stebaev, 1963), on trees (Broadhead, 1958; Kimmel and Meglitsch, 1969), in the sea and on its shores (Colman, 1939), and even on living beetles (Gressitt *et al.*, 1965) and molluscs (Peake and James, 1967). They associate on mountain tops (Mani, 1962), in the tropics (Kettlewell, 1959) and in Arctic and Antarctic regions (Gressitt and Shoup, 1967). It may thus safely be stated that wherever lichens occur, invertebrates will be there with them: in fact, the two groups of organisms are sometimes dispersed by the same mechanism —wind—and thus settle together in remote habitats (Cuénot, 1949; Kühnelt, 1976).

As already stated, many lichen-associated invertebrates have the physiological means to survive periods of desiccation. This characteristic has great survival value for colonizing animals, and undoubtedly exerts considerable selection pressure on invertebrates deposited on lichens by wind dispersion. This mechanism is also of considerable value to animals living on aquatic lichens (Morton *et al.*, 1957; Wieser, 1963). In fact, the ability to withstand intermittent wet and dry periods is probably the single most important factor determining the ability of invertebrates to survive and flourish on lichens.

B. Lichen-locating by Invertebrates

Winds are a major agency in transporting the lichen fauna to its host plants; this factor accounts for the passive lichen "finding" by most of the unspecific aquafauna. Specific lichen associates, like mites, moths and molluscs, must actively seek out their hosts; the search may be at the level of the habitat, more definitely at that of cryptogams in general, or for one lichen genus or species in particular. Travé (1963) presented evidence for habitat specificity in lichenophagous cryptostigmatids; *Pirnodus detectidens* lives exclusively on rock-encrusting lichens; whereas *Dometorina plantivaga* lives in corticolous ones (Fig. 3). *Ameronothrus maculatus*, a related mite, feeds on various lichens which grow together in the *Aspicilietum calcareae* (syn. *Caloplacetum heppianae*) in London (Laundon, 1967). Observations on mites which prefer lichens to moss, and vice versa, were made by Travé (1963).

A rare case of apparent lichen preference by a grazer due to the former's mechanical properties was described by Plitt (1934). The zebra snail, *Oxystyla undata*, prefers to feed on the crustose *Pertusaria amara*, a lichen producing a bitter taste to man. This preference was thought, but not tested, to stem from the fact that the snail could not hold and rasp foliose and fruticose lichens as effectively as the crustose species. Further evidence for the attraction of invertebrates to specific lichens is lacking, but the frequently voiced observation that lichen-mimicking moths manage to alight on the correct, camouflaging plant is rather suggestive. There are several hundred tree species in eastern Brazil, whose trunks are covered by "white, red and greenish" lichens, and each colour is exploited by insects for camouflage (Kettlewell, 1959). It is inconceivable that moths will indiscriminately come to rest on any of these lichens, because they will quickly be eaten by predators; in order to exploit the multicoloured backgrounds, they must alight on the "correct" lichen(s). This presumes some mechanism by which the moths (as well as other camouflaged arthropods) actively seek out and recognize "their" lichens. Some recognition is probably visual, as moths are known to have colour vision (Wigglesworth,

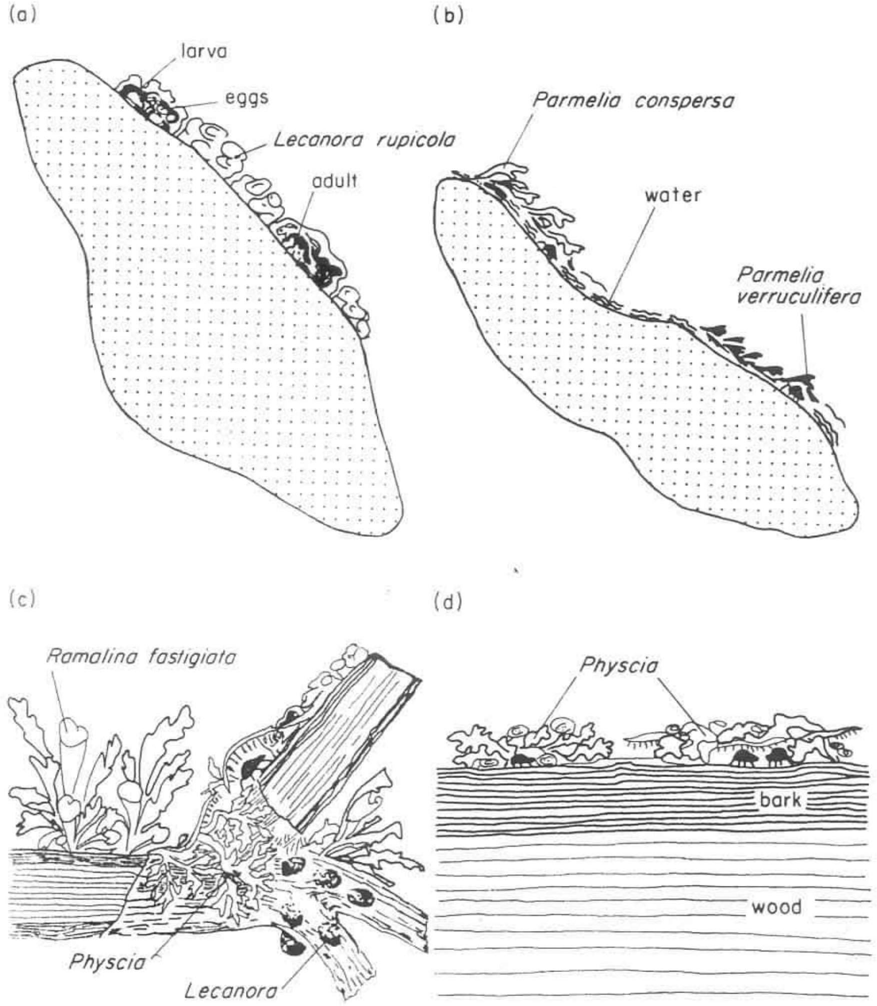

FIG. 3. Simple populations of lichen associated cryptostigmatid mites. (a) *Pirnodus detectidens* on a rock; (b) *Provertex delamarei* on a rock; (c) *Dometorina plantivaga* on an oak branch; (d) *Mycobates parmeliae* on a tree trunk (from Travé, 1963).

1972). However, it is difficult to envisage each moth species finding its "own" lichen during the scanty dawn light. Some supplementary mechanism is a possibility. The "secondary plant substances thesis" of Fraenkel (1959) could be invoked for this purpose and applied to lichens.

Fraenkel (1959) argued that "secondary" plant substances (such as glucosides, saponins, tannins and alkaloids) which only occur inconsistently in plants, have no basic metabolic function in them, and thus are unlikely to have any basic metabolic function in insects also. As many of these substances are inhibitory or toxic towards insects, it may be argued that this was one purpose for which they were evolved or preserved in plants. The fact that many "secondary" substances possess characteristic odours and tastes, as compared to their lack in "primary" (occurring in all plants) substances, lends much support to this theory. Some insects, and possibly other phytophagous invertebrates, have overcome the repellent properties of plants to gain new, and often exclusive, plant hosts. Furthermore, selection has caused the new plant-specific species to become dependent solely on the smell and taste of these secondary plant substances; hence the origins of oligophagy in many insects. We know of no experimental evidence that lichens actually attract certain feeding and mimicking species. Nevertheless, this theory is mentioned because it fits many of the known facts. It is of historical interest that Stahl (1904), who conducted studies on lichen feeding by snails, was actually the first to formulate the theory that plant substances serve to protect them from grazers (cf. Fraenkel, 1959).

C. Lichen Dispersal by Invertebrates

Ants were observed by Bailey (1970) to carry one to three soredia each of *Lecanora conizaeoides*. Beetles with cryptogam gardens, including lichens, were described by Gressitt *et al.* (1965). Mites, *Tricheremenmaeus serratus*, have recently been found in Scotland with soredia of *Lepraria incana* on the hairs of their backs, and would therefore appear to be aiding the lichen's dispersal (Laundon, *in litt.*). Springtails which overrun colonies of *Pertusaria amara* become powdered with their soredia (Ridley, 1930). Various lacewings carry lichen fragments in their "packets" (Skorepa and Sharp, 1971) or on their entire bodies. In the latter case, as the larvae moult, large groups of soredia are left behind with the cast skins (Garrett, 1974). The cases of moth caterpillars may become covered by lichen fragments (Weber, 1974), as do the slimy bodies of snails and slugs.

Lichen-feeding molluscs may void viable algae, which can grow on the faeces (Kühnelt, 1976). The rotifer, *Philodina*, isolated from *Xanthoria*, was observed to ingest ascospores (Pyatt, 1968). Not all ascospores were digested, and upon splashing, the rotifers could be removed from the lichens, whereupon the animals liberated viable ascospores—another, albeit complicated, method of dispersal.

Further aspects of lichen dispersal by invertebrates are covered by Gerson (1973) and Bailey (1976).

V. Invertebrate Feeding on Lichens

A. Modes of Feeding

Most invertebrate lichen feeders ingest their food by chewing or by scraping. Lichenophagous insects, such as barklice, springtails and moth caterpillars, possess mandibulate mouth parts, with which they bite off their food and chew it.

Acari have chelicerate mouth parts, but the most important lichen feeders, members of the Cryptostigmata, possess a mandibula-like modification, the rutella. These are modified setae which sometimes occur as massive dentate structures capable of scraping solid food off its substrate and particulating it (Evans *et al.*, 1961). Prostigmata (gall mites included) have sharp chelicerae with which they pierce plant cells and suck out their contents.

Gastropods obtain their food by scraping it off by means of a toothed, chitinous radula (Owen, 1966). Snail injury on lichens can usually be recognized by the linear scraping pattern of the radula (Peake and James, 1967). Most feeding consists of tearing or scraping off bits of lichen while the feeder is stationed on the plant. Some species, however, feed within the lichens (Brightman, 1965; Holloway, 1970), where they may excavate intricate burrows (Grandjean, 1950). Feeding (especially by gall mites) may result in abnormal growth forms, usually called galls (Grummann, 1960). Another mechanism of gall formation was described by Schade (1933): some feeders may devour only algal cells and consequently the mycobiont overgrows the phycobiont (or its remnants), causing strange growth shapes and forms to appear. Several new lichen species and varieties, especially in the genus *Rhizocarpon*, were described, which are actually no more than well known species damaged by snails and mites (Schade, 1933). Apothecial regeneration of "*Lecanora subfusca* var. *allophana*" due to the gnawing of hymenia by insects has been recorded by Bouly de Lesdain (1924). Molluscs, especially *Clausilia* spp., show a preference for the green algal morphotype of *Sticta canariensis* rather than the blue-green algal morphotype, "*S. dufourii*" (James and Henssen, 1976).

B. Digestion

Very little has been published about lichen digestion by invertebrates, beyond the observation that some species digest the entire symbiont, whereas others only the phycobiont or the mycobiont. The isopod *Campecopea hirsuta* feeds almost exclusively on the phycobiont of *Lichina* *pygmaea*, voiding blue-green faecal pellets (Wieser, 1963) which attest to the digestion of the algae. On the other hand, live algal cells may pass unharmed through the alimentary tract of some lichen-feeding snails, dead algae as well as fungi being digested (Schmid, 1929). Peake and James (1967) argue, from a literature survey, that it is very difficult to determine which symbiont of the lichen, if any, is actually preferred by molluscs.

Possession of enzymatic systems which break down lichenin in arthropods, oligochaetes and molluscs was demonstrated by Holden and Tracey (1950) and by Nielsen (1963).

Woodring and Cook (1962) surface-sterilized eggs of the cryptostigmatid *Ceratozetes cisalpinus* and found that the emergent larvae were unable to feed on sterilized food. However, upon being placed in a culture tube with a few live fungal hyphae, the aseptic larvae fed and continued to develop. These results might be interpreted to indicate the necessity of some specific diet attractant for the mite; in view of the fact that surface-sterilized older mite stages did feed on the aseptic lichen, this explanation cannot be accepted. Another possibility is that the hyphae were required to induce the production and secretion of appropriate lichen-digesting enzymes.

Some Cryptostigmata may carry internal symbiotic microorganisms (Woodring, 1963). Their occurrence is more likely in animals which feed exclusively on a single diet, and some strict lichen feeders may indeed possess such organisms. It is only in ruminants, like reindeer, that lichen-digesting symbiotic protozoa are actually known (Scotter, 1965). However, there appear to be no lichen-specific protozoa in the rumen of lichen-feeding ruminants (Hobson, *in litt.*).

The uptake of diverse heavy metals by lichens is well known. It would be of interest to know whether these heavy metals affect lichen edibility and digestibility by invertebrates. Examination of many thalli of *Lecanora muralis* with high metal concentrations failed to reveal any damage due to invertebrates grazing (Seaward, 1972). Only the clover mite, *Bryobia praetiosa* was found to be associated with this lichen in reasonable numbers from a few sites; however, since members of the genus *Bryobia* are known to feed on higher plants, and *B. praetiosa* infests grasses etc., it seems more probable that this species was sheltering in, rather than feeding on, the lichen (see also p. 102).

Most invertebrates feed only on wet lichens. In some cases (e.g. slugs) this is probably connected with the need of these grazers for humidity, but in others it possibly adds to the ease with which the lichen can be scraped or chewed. Wet lichens are perhaps more edible and more easily digested. On the other hand, dry, gelatinous lichens are almost never attacked by invertebrates. The subject of lichen resistance to grazers will be discussed in the next section.

C. Lichen Resistance to Invertebrate Feeders

The controversy regarding the role of lichen products in protecting lichens against various grazers was summarized by Smith (1921, pp. 395–396):

> It has been argued by Zukal (1895) that the great formation of acid substances in lichens is for shielding them against the attacks of animals; Zopf (1896) on the contrary insists that these substances afford the plants no real protection. He made a series of experiments with snails, feeding them with slices of potato smeared with pure lichen acids. Many snails ate the slices with great readiness even when covered with bitter acids such as cetraric, or with those which are poisonous for other animals such as rhizocarpic and pinastrinic. The only acid they refused was vulpinic, which is said to be poisonous for vertebrates. The crystals of the acids passed unchanged through the alimentary canal of the snails, and were found in masses in the excreta. They were undissolved, but, enclosed in slime, their sharp edges did no damage to the digestive tract.
>
> Stahl (1904) however upholds Zukal's theory of the protective function of lichen acids against the attacks of small animals. Some few snails, caterpillars, etc., that are omnivorous feeders consume most lichens with impunity, and the bitter taste seems to attract rather than repel them; but many others he contends are certainly prevented from eating lichens by the presence of the acids. He proved this by soaking portions of the thalli of certain bitter species for about twenty-four hours in a one per cent soda solution, which was sufficiently strong to extract the acids. He found that these treated specimens were in most cases preferred to fresh portions that had been simply moistened with water.
>
> Even the omnivorous snail, *Helix hortensis*, was several times observed to touch the fresh thallus and then creep away, while it ate continuously the soda-washed portion as soon as it came into contact with it. Calcium oxalate, on the other hand, formed no protection; omnivorous feeders ate indifferently calcicolous lichens such as *Aspicilia* [=*Lecanora*] *calcarea* and *Lecanora saxicola* [=*L. muralis*], whether treated with soda or not, but would only accept lichens with acid contents, such as *Parmelia caperata*, *Evernia prunastri*, etc., after they had been duly soaked.
>
> Experiments were also made with wood-lice (*Oniscus murarius*), and with earwigs (*Forficula auricularia*), and the result was the same: they would only eat bitter lichens after the acids had been extracted by the soda method. Stahl therefore concludes that acids must be regarded as eminently adapted to protect lichens which otherwise, owing to their slowness of growth, would scarcely escape extinction.

A few more recent cases which demonstrate some degree of protection against representatives of various invertebrate groups will be briefly discussed below.

The two common lichenophilous psocid species (*Reuterella helvimacula* and *Elipsocus mclachlani*) occurring on larch trees in northern England show an interesting difference in food preference (Broadhead, 1958); both species graze *Lecanora conizaeoides*. The nymphs and adults of *Reuterella helvimacula* graze the entire surface of the lichen, taking both the apothecia and the algal layer of the thallus indiscriminately. In contrast to this, the nymphs and adults of *Elipsocus mclachlani* graze the apothecia only. No indication was obtained either in the field or in the laboratory that this species ever grazes the thallus of the lichen. The hymenium and the algal layer immediately below it are eaten to expose the white medulla. Broadhead considered that a lichen substance rendered the thallus unpalatable to *E. mclachlani*. However, the major substance in this lichen is now known to be fumarprotocetraric acid which is present in both the apothecium and thallus, so the reason for this discrimination remains obscure. The collembolan *Hypogastrura packardi* feeds only on the upper cortex and most of the algal layer of *Parmelia baltimorensis*, leaving the medulla largely untouched (Hale, 1972). Presence of protocetraric acid in the medulla was believed to protect the lichen from its grazer. Gressitt and Shoup (1967), working in the Antarctic, noted that the oribatid *Maudheimia petronia* feeds only in the stem and base of the fruticose *Usnea antarctica*, feeding being apparently restricted to the "white portions" of the lichen.

Browsing on various lichens by the slug *Lehmannia marginata* was reported by Coker (1967). *Lobaria pulmonaria*, *Hypogymnia physodes* and *Pertusaria pertusa* were all grazed, but apothecia were preferred to the cortex in the latter lichen. However, *Pertusaria amara*, growing in association with *P. pertusa*, was not affected.

A list of some invertebrates reported to feed on lichens, together with the latter's secondary products (culled mainly from Culberson, 1969, 1970; Table III), raises more questions. Fumarprotocetraric acid may partially protect *Usnea "barbata"* from *Maudheimia petronia* (Gressitt and Shoup, 1967). On the other hand, the psocid *Reuterella helvimacula* freely grazes on *L. conizaeoides* (Broadhead, 1958; Seaward, 1965), and the mite *Phauloppia lucorum* feeds on *Cladonia fimbriata* (Seaward, 1974), which also contains fumarprotocetraric acid. This substance further occurs in *Cladonia ochrochlora*, which is damaged by an unidentified gall maker (Bachmann, 1929). The lichen acid thus affords, at best, only partial protection against grazers. Another similar example is picrolichenic acid, apparently specific to the genus *Pertusaria* (Culberson, 1970). It probably renders *P. amara* unpalatable to the slug *Lehmannia marginata*, but another molluscan,

TABLE III.

Invertebrates and the lichens they feed upon. Data pertaining to lichen acids, mainly from Culberson (1969, 1970).

Invertebrate	Lichen	Lichen compounds	Source
Cryptostigmata:			
Ameronothrus maculatus	*Candelariella medians*	calycin	Laundon (1967)
A. maculatus	*Physcia caesia*	atranorin, zeorin	Laundon (1967)
A. maculatus	*P. orbicularis*	rhodophyscin (±)	Laundon (1967)
Dometorina plantivaga	*Caloplaca ferruginea*	emodin, fallacinol, parietin, parietinic acid	Travé (1969)
D. plantivaga	*Lecanora subfusca* agg.	atranorin	Travé (1969)
D. plantivaga	*Pertusaria hymenea*	thiophanic acid, gyrophoric acid (±)	Travé (1963)
Maudheimia petronia	*Usnea antarctica*[a]	fumarprotocetraric acid, usnic acid	Gressitt and Shoup (1967)
Phauloppia lucorum	*Cladonia fimbriata*	fumarprotocetraric acid	Seaward (1974)
P. lucorum	*Parmelia saxatilis*	atranorin, lobaric acid, salazinic acid	MacNeill (1966)
P. lucorum	*Xanthoria parietina*	atranorin, parietin, parietinic acid	Seaward (1974)
Pirnodus detectidens	*Pertusaria rupicola*	norstictic acid, stictic acid, thiophaninic acid	Travé (1969)
Psocoptera:			
Cerobasis guestfalicus	*Xanthoria parietina*	atranorin, parietin, parietinic acid	Seaward (1965)
Elipsocus mclachlani	*Lecanora conizaeoides*[a]	fumarprotocetraric acid	Broadhead (1958)
Mesopsocus immunis	*Lecanora conizaeoides*	fumarprotocetraric acid	Seaward (1965)
Reuterella helvimacula	*Hypogymnia physodes*	atranorin, chloroatranorin, physodalic acid, physodic acid	Laundon (1971)
R. helvimacula	*Evernia prunastri*	atranorin, chloroatranorin, evernic acid, usnic acid	Laundon (1971)
Mollusca:			
Lehmannia marginata	*Hypogymnia physodes*	atranorin, chloroatranorin, physodic acid, physodalic acid	Coker (1967)
L. marginata	*Lobaria pulmonaria*	constictic acid, norstictic acid, stictic acid	Coker (1967)
Oxystyla undata	*Pertusaria amara*	picrolichenic acid, fumarprotocetraric acid (±)	Plitt (1934)
O. undata	*Lecanora pallida*	atranorin, norstictic acid, protocetraric acid	Plitt (1934)

[a] Denotes partial feeding.

Oxystyla undata, thrives on this lichen (Plitt, 1934), and *P. albescens*, which also contains picrolichenic acid, is devoured by the mite *Dometorina* (Travé, 1963). It is known that different lichen substances are restricted to different parts of the same lichen (e.g. cortex v. medulla), as reviewed by Hawksworth (1976).

Hale (1972) attributed the protection of the medulla of *Parmelia baltimorensis* from a collembolan grazer to the presence of protocetraric acid in that region. This acid, as well as fumarprotocetraric acid, is a depsidone (Culberson, 1969), and substances belonging to this group could thus be expected to serve as lichen protectants. However, norstictic, physodalic, salazinic and stictic acids are also depsidones, occurring in lichens such as *Pertusaria pertusa*, *Lobaria pulmonaria* and *Hypogymnia physodes*, which are grazed by various invertebrates.

It thus appears that the whole subject of "protection from grazers" is still full of contradictions, and no general theory can as yet be formulated. Lack of experimental data as well as information on the quantitative and qualitative distribution of the acid within the various lichens hinders such a formulation.

Several mechanisms have been proposed to account for the widely reported lichen resistance to invertebrates. These mechanisms include the specific effect of lichen acids, the protective, gelatinous covering of some lichens, and the presence of chelating agents in many lichens (Gerson, 1973). The effect of lichen acids is probably made up of several factors, such as solubility, reduced palatability, outright toxicity and possible indirect toxicity mediated through the antibiotic effect of some acids on the symbiotic microflora of certain invertebrate grazers. A fourth component may well be the acidic environment, in part formed by lichen acids released into the soil substrate. Gadea (1964a, 1973) believed that *Xanthoria* and *Roccella* thus inhibit some soil animals, especially nematodes.

Certain extracts have in fact been found to be active against microorganisms, and have served as the basis of a modest lichen antibiotic industry. The possibility of using such extracts against insect pests was explored by Heal *et al.* (1950), within a broad survey of plants for insecticidal activity. Aqueous extracts of *Cetraria juniperina*, *Letharia vulpina*, *Lecanora rubina*, *Parmelia perforata*, *Peltigera canina* and *Lobaria pulmonaria* were all toxic to American cockroaches (*Periplaneta americana*) when injected into their bodies. But immersing German cockroaches (*Blattella germanica*) and milkweed bugs (*Oncopeltus fasciatus*) into most of these extracts did not affect the insects. Chloroform extracts of *Cetraria juniperina* and *Lecanora rubina* were very toxic to larvae of the black carpet beetle (*Attagenus piceus*), but not to German cockroaches, milkweed bugs and larvae of the webbing clothes moth (*Tineola bisselliella*) and of the mosquito *Anopheles*. On the other hand, the larvae of the mosquito *Aedes* were affected by the chloroform extract of *Lecanora rubina*. One may thus conclude that lichens are not promising source material for insecticides.

Other invertebrates are also known to be affected by lichen products. Richardson (1975), citing Russian sources, states that a sodium salt of usnic acid ("Binan") is used in Russia against the protozoan *Trichomonas* which is parasitic in man and infests the lower reproductive tract. An acidic extract of *Xanthoria parietina* was reported by Grzyb (1964) to inhibit development of the egg of the common pig roundworm (*Ascaris suum*). However, as extracts of other lichens had no effect on these eggs, it was concluded that such extracts have little applied value.

Some lichen chemicals were used extensively in the past, and are to a limited extent used today, as dyestuffs. One wonders whether garments dyed with these lichen extracts were indeed more resistant to clothes moths. This question is of some evolutionary interest, as larvae of certain members of the clothes moth family, the Tineidae, feed on lichens.

D. Energetics of the Lichen Fauna

Studies on the energetics of various plant and animal communities are coming more and more to the forefront of current ecological research. Engelmann (1966) presented a lucid discussion of productivity and the kinds of information needed for the study of animal energetics. Various estimates are required: ingestion, assimilation, egestion, respiration, growth and death rates of the relevant fauna, its numbers and biomass, and the energy units represented by these figures.

Little work on the energetics of lichens has been published to date; most of it has been summed up by Wielgolaski (1975). Thus, maximum lichen biomass in southern alpine Norway comes to about 1200 g m^{-2} in unshaded, not too dry ridges. At the central Hardangervidda plateau the dry weight biomass of lichens, dominated by *Cetraria nivalis*, usually comes to 200–400 g m^{-2}. The annual primary production of lichen heaths totally dominated by lichens is only about 100 g m^{-2} even in dense mats. The production to biomass ratio in lichens in this area is about 0·2. No data are available on specific invertebrate lichen feeders. Several species, or their close relatives, which include lichens in their diet, have been investigated in this context (Slobodkin and Richman, 1961; Engelmann, 1966) and reviewed by Harding and Stuttard (1974). Speculative energy balance sheets could thus perhaps be drawn up, but this appears to be premature. A specific problem is the intermittent, humidity-dependent development of several lichen feeders, as discussed above. Too little is known about the metabolism of these grazers to make any effort at energetics study worthwhile, but it appears useful to compile and summarize one kind of relevant data, namely quantitative information on lichen invertebrates.

Most available data come from ecological studies of Arctic and Antarctic regions, probably because lichens are such an important floral component there. Watson *et al.* (1966), reporting on Alaskan terrestrial invertebrates, included an unidentified lichen community in their observations. The community was sampled from June to September (Table IV), and Collembola were, on a yearly basis, more than twice as abundant as mites. In another study (Bengtson *et al.*, 1974), soil invertebrates were sampled in several

TABLE IV.

Collembola and Acari (per m^2) obtained from a lichen community, Cape Thompson Region, Alaska (from Watson et al., *1966).*

Date	No. of samples	Collembola (±s.e.)	Acari (±s.e.)
June 21	4	12,900 ± 2780	7840 ± 938
July 10	4	12,800 ± 3410	10,500 ± 921
July 24	4	15,200 ± 4110	5240 ± 984
August 8	4	37,600 ± 9440	8340 ± 1580
August 21	4	4240 ± 1170	6440 ± 1390
September 8	4	14,400 ± 7740	6780 ± 1430
September 18	3	5330 ± 2670	5990 ± 2330

TABLE V.

Collembola and Acari (per m^2) obtained from four different plant communities in Spitsbergen (from Bengtson et al., *1974).*

	Collembola (±s.e.)	Acari (±s.e.)
Cetraria spp.: vegetation and litter	9510 ± 784	16,192 ± 1874
soil (0–3 cm)	11,288 ± 2604	5117 ± 1094
Cetraria spp.: vegetation and litter	27,091 ± 1929	19,195 ± 1850
soil (0–3 cm)	11,180 ± 1485	5031 ± 2521
Moss (*Drepanocladus* spp.)	243,475 ± 1921	22,090 ± 1667
Grassland	268,830 ± 24,727	247,880 ± 19,606

Spitsbergen plant communities (Table V); Collembola were again more abundant in lichens (*Cetraria* spp.), but were still low in numbers as compared to the moss and grassland fauna. Mites, on the other hand, did not become more abundant in moss; this suggests that the cryptogams have a similar "carrying capacity" for mites, but lack of additional data on the mites and their diets renders such information of limited value from the energetics point of view.

Gressitt (1967) collected invertebrates from rock-encrusting lichens in the maritime Antarctic and obtained somewhat different results (Table VI): Acari (consisting mainly of three cryptostigmatid and one prostigmatid species) outnumbered Collembola.

Working in the South Ural Mountains, Stebaev (1963) sampled invertebrates in sparse and dense rock-encrusting *Parmelia centrifuga* stands with a northern and a southern aspect. His data (Table VII) again show that

TABLE VI.

Average (and maximum) sample counts of arthropods obtained from various microhabitats in the Antarctic Peninsula–South Shetland Islands–South Orkney Islands area, and processed through Berlese funnels (from Gressitt, 1967, his Table 2).

	Usnea	*Ramalina*	*Physcia*	*Caloplaca/ Xanthoria*	*Umbilicaria*
Acari: Mesostigmata					
Cyrtolaelaps racovitzai	–	1	21	–	–
Acari: Prostigmata					
Stereotydeua villosus	–	–	4	–	–
Tydeus tilbrooki	18	150	110	250	–
Acari: Cryptostigmata					
Oppia loxolineata	0·1	–	–	–	–
Alaskozetes antarcticus	0·1	1	115	3	–
Halozetes belgicae	53	2	60	75	–
Magellozetes antarcticus	64	–	138	37	2
Insecta: Collembola					
Cryptopygus antarcticus	0·1	–	–	–	–
Archisotoma brucei	–	–	0·6	–	–
Parisotoma octooculata	–	2	2	–	–
Belgica antarctica	–	–	12·2	–	–
Total	135·3	156	462·8	365	2
Maximum population in single sample	450	209	1158	542	2

TABLE VII.

Arthropods (per dm²) in sparse (Cycle IIa) and dense (Cycle IIb) colonies of saxicolous Parmelia centrifuga *(from Stebaev, 1963).*

Arthropods	South		North
	Cycle IIa	Cycle IIb	Cycle IIb
Acari:			
Prostigmata	25·0	174·0	28·0
Cryptostigmata	692·5	486·0	900·0
Collembola	237·5	1148·0	410·0
Diptera	50·0	135·0	5·0

Acari (especially Cryptostigmata) and Collembola are the dominant arthropods there. Upon comparing these data with those of Watson *et al.* (1974), it becomes apparent that the South Ural lichen fauna is much richer in numbers. Seaward (1974) estimated about 23 *Phauloppia lucorum* (Cryptostigmata) to be present in 1 cm² of lichen; in other words, about 230,000 m^{-2}. This is more than ten times the number obtained in Alaskan and Spitsbergen work, and also considerably higher than Stebaev's figures. Although the habitat and climatic conditions are quite dissimilar, one should emphasize the different community sizes studied in the interpretation of these data.

Colman's (1939) paper is still the best source for numerical data on invertebrates living on and in marine lichens (Table VIII—assembled

TABLE VIII.

Invertebrates on Lichina pygmaea *(from Colman, 1939).*

Animal group	Individuals/100 g *Lichina*	Individuals/m² rock surface
Oligochaeta	11	220
Cirripedia	287	5740
Isopoda	2886	57,720
Amphipoda	35	700
Acari	436	8720
Insecta	161	3220
Bivalvia	9447	188,940
Gastropoda	453	9060
Total	13,716	274,320

from sections of Tables XX and XXII in Colman, 1939). He also reported that 1 m^2 of *Lichina pygmaea* weighs 2 kg and that the most abundant animal on the lichen is the bivalve *Lasaea rubra*. Although Colman's values for *L. rubra* were quite high, Morton (1954) found even denser populations: he reported that 15 cm^2 of *Lichina pygmaea* tufts yielded close to 900 *Lasaea rubra*. This is equivalent to over half a million individuals per m^2 of the lichen.

TABLE IX.

Number of species, density, biomass and respiration of Acari and Collembola (excluding carnivores) collected in crustose lichen habitat on Signy Island, Antarctica (from Collins et al., *1975).*

		Collembola	Acari	Total
No. of species		1	6	
Density ($\times 10\ m^{-2}$)	Summer	7	39	
	Winter	<1	40	
	Annual mean	4	40	
Mean annual biomass (mg wet weight m^{-2})		100	2408	2508
Total annual respiration ($cm^2\ O_2\ m^{-2}$)		105	1021	1126

Weight (or biomass) of many invertebrate groups which occur in lichens is actually available. Healey (1967), Engelmann (1968), and Harding and Stuttard (1974), among others, compiled data on the biomass and respiration of nematodes, mites and springtails. Collins *et al.* (1975) provided similar information on the fauna of the maritime Antarctic; some of their data are given in Table IX. The main components that are still missing are energetics data on the lichens themselves, and physiological studies on their grazers. Barrett and Kimmel (1972) advocated using lichen-bearing tree bark ecosystems for energy-flow and mineral–recycling studies, in view of the simplicity and accessibility of such systems. An early model of the kind of study needed was presented by Golley (1961), who obtained energy values for an entire community, including diverse plants (and their different parts) and invertebrates, on a monthly basis.

E. Food-webs and Nutrient Recycling

Lichens serve as the basis of food webs in which lichenophagous species serve as primary consumers, being in turn devoured by various predators, but very little is known about these relationships. *Loricula elegantula*, a predacious bug (Microphysidae) lives in lichens, especially *Parmelia* spp., where it deposits its eggs; the larvae and adults feed on mites and psocids (Southwood and Leston, 1959) including the lichenophagous barklouse *Reuterella helvimacula*. Pseudoscorpions feed on lichen-grazing psocids which live on shrubs in the Chaco region of Argentina (Morello, 1970). Many general predators which occur in lichen colonies and presumably feed on the indigenous fauna were listed, among others, by Cott (1957), Mani (1962) and Stebaev (1963).

A special case which involves an entomogenous fungus was mentioned by Cunningham (1907) from Bengal. The bark of *Oreodoxa* palms is overgrown by multicoloured lichens, upon which many psocids browse; they, in turn, are heavily attacked by a fungal disease.

Air pollution adversely affects epiphyte populations, and therefore diminishes their grazers. Gilbert (1971), in a study on the fauna of corticolous lichens, bryophytes and algae, found that primary consumers (mostly psocids) were reduced in an air-polluted area. The predators, on the other hand, survived in their usual numbers, probably by feeding on alternative prey. The effect of diminishing lichen "pastures" on specific predators and parasitoids was not studied.

Lichens are well known for their ability to absorb large quantities of heavy metals and radioactive elements (James, 1973; Tuominen and Jaakkola, 1974). Thus it is to be expected that such chemicals would be passed on in food-webs. The lichen–caribou–man food-chain maintains high radionuclide levels in Alaskan residents, but nothing is known concerning the effects of these compounds on invertebrates. Nor has anything been published about the effect of heavy metal concentration in lichens on their grazers.

Pesticides are another group of chemicals which may accumulate in food-webs. A pertinent case was recounted by Shilova *et al.* (1973) from subarctic Siberia: the insecticide Sevin (1-naphthyl *N*-methylcarbamate, also known as carbaryl) was applied there against blood-sucking flies, and was afterwards found at various trophic levels, reaching 0·5 p.p.m. in the lichens assayed.

Barrett and Kimmel (1972) suggested that lichen-bearing tree bark might be a suitable ecosystem for studying energy flow and mineral recycling. This was indeed done by Denison (1973) in Douglas fir forests in Oregon. *Lobaria oregana* is the most abundant lichen in the tops of these trees; it fixes atmospheric nitrogen through one of its phycobionts, the blue-green alga *Nostoc*. Denison (1973) estimated that *L. oregana* contributes 1·8–10·0 lb N acre^{-1} ($=2{\cdot}0$–$11{\cdot}1$ kg ha^{-1}) per annum to the fir forest ecosystem (cf. Forman, 1975). A major part of this element reaches the soil through the fall and decay of *L. oregana*; another route is by animal feeding, including nematodes, mites and insects.

Frankland (1974), while discussing decomposition of lower plants, stated that nothing is known about lichen decomposition: whether it is by autolysis, weathering or microbial activity. Decomposition, in the broad sense, is considered to have two components: these are mechanical breakdown, often mediated through invertebrates, and chemical decomposition, brought about by microbial action. The significance of breakdown to decomposition stems from the grazing and burrowing activity of invertebrates, which exposes innumerable new, often formerly impenetrable, surfaces to the action of decomposing microorganisms. Invertebrates which graze on lichens thus contribute to the plants' decomposition.

Lichen breakdown is described by Hale (1972): the collembolan *Hypogastrura packardi* completely chews away the upper cortex and most of the algal layer of *Parmelia baltimorensis*. Consequently, large areas in the lichen centres were disintegrating and falling away, resulting in a loss of at least half the lichen colony. Additional cases of lichen breakdown by invertebrates have been described by Schmid (1929), Denison (1973) and Laundon (1967, 1971) among others. Feeding and burrowing by these grazers cause additional, often unprotected lichen surfaces to be exposed to other microorganisms. They also entail some vertical and (when feeding upon terricolous lichens) horizontal redistribution of lichen fragments.

An indirect mechanism of lichen breakdown through insect activity was described by Llano (1956) from Arctic regions. Reindeer which graze in lichen pastures during dry periods cause excessive thallus fragmentation by trampling on them during their short rapid runs windward, intended to shake off blood-sucking insects.

These few examples suffice to show that invertebrates, whether directly or indirectly, play a particular role in lichen breakdown and decomposition. Quantitative data, however, are not available.

VI. Lichens as a Protective Environment for Invertebrates

As one surveys the variety of invertebrate life associated with lichens, and considers the great abundance of these plants on trees, walls, stones and soil, it is not surprising that lichens often serve as shelter for invertebrates. In its simplest form, this merely means that invertebrates hide under lichens; no special adaptations are involved. After prolonged sheltering in this microhabitat, some invertebrates were no doubt favoured by evolving various forms of adaptive coloration. This blending of the animal into its lichen background can be brought about by camouflage and by mimicry. Camouflage may consist of lichen fragments and soredia, or of the entire plant growing on the animal. Evolving along another route, invertebrates mimic lichens by their very appearance. This adaptation, especially well developed in moths, met a severe challenge during the Industrial Revolution, when the ascendancy of melanic morphs provided a fascinating glimpse of evolution in action.

A. Concealment

Lichen colonies on rock and tree bark provide a buffer zone between certain invertebrates and their environment. Economic entomologists have noted the presence of pests underneath lichens and stated that these have to be removed in order to control the pests. The Italian pear scale, *Epidiaspis leperii* (Homoptera, Diaspididae) is a pertinent case. This pest is often overlooked because it is hidden under lichens on fruit trees. Control recommendations include caustic soda, which is added to the spray in order to remove the protecting lichens (Essig, 1958). Similar pest control using a tar oil wash on lilac trees has recently been observed in Ireland (M. R. D. Seaward, unpublished). Colonies of the pear phylloxera, *Aphanostigma pyri*, a serious pest of pears in Israel, were observed to thrive under *Xanthoria parietina* on otherwise clean pear branches in Israel (U. Gerson, unpublished). Some pests, like the hemlock loopers, *Lambdina fiscellaria fiscellaria* and *L.f. lugubrosa* (Lepidoptera), lay their eggs on epiphytic moss and lichen patches (Thomson, 1958; Jobin, 1973; Brodo and Hawksworth, 1977). Pupation of the Assam thrips, *Scirtothrips dorsalis*, takes place in similar habitats (Dev, 1964). Lichens provide winter sanctuary for many phytophagous insects and mites, an example of the latter being *Bryobia* (Tetranychidae) (Travé, 1963). During the later stages of the 1976 ladybird (*Coccinella* spp.) "invasion" in the British Isles, lichens provided an effective shelter, and, for example, counts of more than 50 specimens beneath many thalli of *Pseudevernia furfuracea* in exposed places at higher altitudes of the Pennines were not uncommon during October (M. R. D. Seaward, unpublished).

Marine invertebrates, like the bivalve *Lasaea rubra*, also find shelter in lichens, although they do not feed on them (Morton *et al.*, 1957).

B. Camouflage

Representatives of at least two insect orders employ what Cott (1957) has termed "masks of adventitious material", which consist of lichen particles.

Larvae of the South American brown lacewing *Hemerobius* cover themselves with mosses and lichens. Hingston (cited by Cott, 1957) describes these larvae:

> . . . one I met was a perfect circle, it was made out of tiny bits of lichen and . . . was an exact image of the round lichenous patches that occur so commonly on forest trees.

This aggressive deception helps *Hemerobius*, a predator, to take its prey by surprise. A North American neuropteron, *Notida pavida*, regularly collects lichen fragments to construct a "packet" which it places on its back; Skorepa and Sharp (1971) present photographs of such lichen-covered larvae. Garrett (1974) found larvae of a Colombian lacewing, *Chrysopa*, covered by soredia of several lichens. The larvae excrete a sticky silk, to which soredia adhere as *Chrysopa* walks across the lichens.

Weber (1974) found two lepidopterous caterpillars in Australia and New Guinea, which were covered with *Parmelia* fragments. In one instance, larval cases of *Cebysa leucoteles*, and in the other, the larvae themselves, of an unnamed Eucleid, were covered with them.

An example of insect camouflage by means of living lichen growth was found by Gressitt (1966) in New Guinea moss forests. This association involves Curculionid beetles (weevils) which support extensive plant growths on their backs. The beetles, mostly of *Gymnopholus* subgen. *Symbiopholus*, are often structurally modified to accommodate the various plants growing on them. These modifications are dorsal depressions surrounded by ridges, specialized setae and scales, and a sticky secretion which apparently promotes plant growth. About 28% of all beetle specimens collected bore conspicuous lichen growths, and another 5–6% primary growths. Ten *Gymnopholus* species supported lichens, the latter being identified as *Parmelia* sp., *P. crinita*, *P. reticulata*, *Anaptychia* sp. and *Physcia* sp. All except the last species were obtained from the aptly named *G. lichenifer*. Lichen colony size on these beetles suggested that the insects were at least 3–5 years old when collected, and this was confirmed by later observations (Gressitt and Sedlacek, 1970). The beetle–cryptogam association is considered to be of mutual advantage, the animals providing a favourable environment for the plants, the latter endowing the insects with protective resemblance, a form of camouflage, to cryptogam-covered parts of vegetation or to inedible plants (Gressitt *et al.*, 1965). The term "epizoic symbiosis" was coined by Gressitt (1966) to describe this association.

Marine lichens, like *Arthopyrenia halodytes* and, more rarely, *Verrucaria* spp., are observed on living molluscs and barnacles. This growth may well be fortuitous, since the lichens are also found on empty shells, and no special adaptations designed to encourage colonization are found. Nevertheless, some survival value of a protective nature may well accrue to the molluscs.

C. Mimicry

> As regards appearance, bark-resembling animals lead up to, and intergrade with, other types which in their most specialized form resemble in high degree the lichens growing on wood or on walls. The resemblance is literally superficial, rather than structural—that is to say, it is generally due to the most ingenious and deceptive disruptive patterns, which give the optical impression of irregular processes and deep interstices—even when painted, as they often are, on the flat canvas of a moth's wing or on the ovoid abdomen of a spider—rather than to actual excrescences and irregularities in the animal's form. From the standpoint of camouflage these cases are therefore of the greatest interest.
>
> Lichen-like species are not confined to any particular continent or country: they may be seen on the limestone walls of a Wiltshire garden or on the slopes of an extinct volcano in Lanzarote; in the luxuriant rain-forests of South America, or on the rocky summit of a Scottish mountain. Nor are they restricted to one phylum or to a few families. Wherever lichen forms a characteristic feature of the environment, different animals are found associated with it for purposes of feeding, of shelter, or of predation; and many of these—including such a diverse assemblage as phalangids and spiders; mantids, stick-insects, and grass-hoppers; moths and caterpillars, weevils and longicorn beetles . . . are decorated in colour (and sometimes modified in form) so that they appear to resemble it, and are most difficult, and often almost impossible, to detect in their natural roosting, feeding, or hunting grounds. (Cott, 1957)

Photographic evidence of arthropods blending into their lichen background is shown by Cott (1957), Kettlewell (1959) and Farb (1963). Morphological modifications of the insect body, in addition to appropriate colour and disruptive patterns, intended to resemble the structure of lichens have seldom been documented. Chopard (1938) mentions a tettigoniid (Orthoptera), *Cymatomera*, whose femora are lobe-like, thus closely resembling lichens which occur on tree bark, and Richardson (1975) mentions South American bugs whose flat bodies resemble lichen thalli.

Cott (1957) pointed out that animals which mimic a certain background also live there; they are usually closely associated with their model. Regarding lichens, resemblance may be restricted to one stage in the development, or it may last throughout the animal's cycle. Some invertebrates only use the lichen background as a sanctuary for rest. Various moths may be mentioned in this context, as well as the flies Bullock (1966) saw resting on saxicolous lichens in Singapore, which simulated sporulating bodies until disturbed. Similar observations involving Collembola on corticolous and saxicolous substrates have been made by Seaward (1975 and unpublished data).

How does a moth or fly "recognize" the appropriate background on which to alight so as to become indiscernible to its predators? Cott (1957) wrote that a moth, whose wings resemble the bark of casuarina, "instinctively" settles with its body in a vertical position, thus bringing the pattern of the wings parallel to that of the bark, which they simulate. Cott also notes that moths whose wings resemble bark cracks settle on the bark in alignment with real cracks.

It is reasonable to postulate that any moth which settles otherwise would quickly be eliminated by predators, consequently selection would favour moths which settle in the "correct" position. Lichens, however, occur in a random pattern and are subject to succession and grazing. How then does a moth "recognize" the lichen or lichens which best suit its own wing pattern? This question becomes of special interest if one considers the situation in Brazil, where, according to Kettlewell (1959), multicoloured lichens occur on diverse trees, and all are utilized for defence mechanisms. Visual substrate recognition cannot be the entire answer. Had moths been able to find their resting sites by sight alone, the typical forms of the peppered moths (see below) would have found some other greenish substrates, and industrial melanism might never have evolved. It may well be that moths (and other insects) are attracted to the odour of specific lichen compounds. Specific moths may also settle on specific lichens in response to specific environmental factors required by the lichen. These could include humidity, temperature and aspect, as well as other stimuli resulting from factors which enable the lichen to settle and grow on any particular site.

D. Industrial Melanism

Industrialization, with its concomitant smoke and soot pollution, has brought about a breakdown in the concealment association between lichens and some insects. Lichens are extremely sensitive to such pollution; trees, rocks and soil, formerly covered by lichens in many parts of northern Europe, have become bare and bleak in industrial centres, subsequently assuming a blackened appearance due to incessant soot deposition. As lichen-covered surfaces were the normal resting places for many cryptic moths, the animals became exposed to visually directed predators, especially birds. The complicated, cryptic colour patterns on the moth's wings, which sometimes closely mimic foliose lichens, evolved under selection for concealment, and became a liability when observed against the newly blackened backgrounds. The mode of survival of many of these species, the best known being the peppered moth, ***Biston betularia***, through the selection and subsequent success of dark, melanic forms, has become known as "industrial melanism" (Kettlewell, 1961).

Kettlewell (1956) showed that in unpolluted areas of British countryside, supporting a rich lichen flora, *B. betularia* occurs mostly in the form *typica*, which is practically impossible to see against a background of lichen-covered tree trunks. The dark, melanic form, *carbonaria*, also occurs from time to time, but due to its conspicuousness on the same lichen-covered trees, it is rapidly eliminated by bird predation. This form is maintained only by recurrent mutations and migration from polluted areas. When smoke and soot intrude, the trees blacken, the lichens begin to disappear, and the form *typica* becomes the more conspicuous of the two, *carbonaria* the better protected. The latter, or an intermediate melanic form, *insularia*, is consequently the dominant form of *B. betularia* in all industrialized and lichen-depleted regions of Britain (Kettlewell, 1973).

Despite these reports based on the association of high frequencies of melanics and absence of lichens, no detailed evidence was formerly available on the role that lichens actually play in determining the frequency of *carbonaria*. Using a method developed by Lees *et al.* (1973), Bishop *et al.* (1975) sampled lichen taxa on oak trunks along a transect from northwest Manchester to north Wales. They also recorded several physical variables, including the light reflectance off trees, and estimated the frequency of the *carbonaria* morph. All these data were subjected to a multiple regression analysis, which revealed the strong relationship between the frequency of melanic moths and lichen diversity. Furthermore they found that at about 75 km from Manchester the number of lichen taxa began to rise dramatically where the percentage occurrence of *carbonaria* declined significantly.

There is strong evidence here to support the hypothesis that the disappearance of lichens due to the increase in air pollution (mainly sulphur dioxide), rather than the direct blackening of substrate surfaces by the particulate matter of the latter (cf. Kettlewell, 1973), may have been the primary cause for the increase in melanic morphs in this species.

Popescu (personal communication) has studied the distribution of the psocid *Mesopsocus unipunctatus* in Yorkshire. This species occurs in two morphs: a light form which is concealed on lichen-covered bark, and a melanic form which blends well with bark blackened by soot. Results of a multiple regression analysis using 12 environmental variables show a significant relationship between increasing populations of the melanics with decreasing lichen cover and with increasing sulphur dioxide and smoke concentrations (cf. Bishop *et al.*, 1975). Lichen cover thus appears to be critical for the maintenance of light-coloured morphs of *Biston betularia* and *Mesopsocus unipunctatus*.

The implementation of the Clean Air Act (1956) in recent years by the establishment of smokeless zones throughout the British Isles opens up some intriguing ecological contingencies. Should lichens return to at least some of their former diversity and abundance, moth melanics would again be at a serious disadvantage, and may suffer a severe eclipse Between 1961 and 1974 the frequency of non-melanics of *Biston betularia* had increased from 5·2 to 10·5% in Cheshire (Bishop and Cook, 1975), and similar increases with this (e.g. Clark and Sheppard, 1966) and other insects have been noted in urban areas elsewhere. A reversal of industrial melanism is probably now taking place in the British Isles.

A further complication arises from the establishment of toxi-tolerant algae and the lichen *Lecanora conizaeoides* which create a monovegetational epiphytic cover and hence a further background (light to dark green) in which to blend. Such a condition, or the return of lichens in limited diversity and (or) abundance, may result in the evolution of another morph of *Biston betularia*. Some clue to this line of development may be provided from research on the morph *insularia* which was first noted in the British Isles about the turn of this century and is now considered to be a non-industrial melanic occurring at a low frequency. This morph appears to be admirably suited for resting on boughs covered with algae; background scoring efficiency gives *insularia* a position intermediate between *typica* and *carbonaria*, but *insularia* has never been found higher than 50% in British populations of *Biston betularia* (Kettlewell, 1973). Nevertheless, *insularia* is on the increase in many areas and is found most frequently at the present time on the edge of industrial areas but outside centres with a high frequency of *carbonaria*, in whose presence it is impossible to detect them phenotypically. Other work has shown areas where melanics are on the increase and those where they are decreasing: high *carbonaria* is found in non-industrial East Anglia and high *insularia* in industrial southwest England and South Wales, so other factors, possibly including climate and lichen diversity, are involved.

VII. Lichen–Invertebrate Communities

A. Terrestrial Colonization

Changes in invertebrate number and diversity during various stages of soil development were studied by Stebaev (1963). He divided the process of soil colonization by animals into discrete cycles. His Cycle II consisted of *Parmelia centrifuga* patches on granite rock. As *Parmelia* grew denser (the shift from Cycle IIa to IIb), there was a notable increase in animal numbers (Table VII). Later on, as mosses replaced the lichens, a substantial increase in invertebrate abundance and diversity took place. Similar observations were made by Gadea (1964c). Summing up his studies of high-mountain moss zoocoenoses, he stated that lichens provide a very poor biotope for the microfauna (aquafauna in the present context). It is only when bryophytes begin to colonize such habitats that animal populations increase.

Some invertebrates still play a lichen-mediated role in the early colonization of certain soils. Schmid (1929) noted the snails *Pyramidula rupestris* and *Chondrina avenacea*, which feed on the endolithic *Verrucaria calciseda* and on *Protoblastenia rupestris*. The snails graze the lichens' thalli and apothecia, voiding undigested algal remains in their faeces, which also contain chalk granules and detached radula teeth. These droppings form a suitable substrate for mosses as well as for higher plants. "From this it follows that snails are of great significance in the colonization of rock surfaces and in this way contribute to soil formation" (Kühnelt, 1976, p. 111).

To sum up invertebrates which live in lichen colonies contribute to soil formation by grazing on the plants, enriching the surrounding area by their faeces and cadavers, and by attracting predators to that site. A further contribution is made by animals which only shelter there.

B. Competition for Settling Sites

Within the littoral zone of rocky shores around the British Isles is a wide, black area of encrusting *Verrucaria* spp. The lichens intergrade with a zone of barnacles; as these are also sessile organisms, some competition for settling sites takes place there (Stephenson and Stephenson, 1972; Fletcher, 1973).

Such competition only appears to be of importance in the initial stages of colonization, because once established, lichens successfully resist further barnacle settlement (Fletcher, 1973). Resistance is therefore due mainly to a mechanical mechanism: young, mobile barnacles (spat) settle on lichen tufts, but few stay there for more than 2 weeks. Fletcher believes that this is due to a general imperfect adhesion of the spat to the lichen's surface. A further mechanism involving some repellent or inhibitory substance(s) produced by the lichens is possible. Any repellent effects can be expected to be more pronounced in larger, and thus older, lichen colonies. Indications of such chemical defence mechanisms are: (1) once established, lichens resist barnacle encroachment, and (2) limpets (*Patella*) which graze on colonizing lichens tend to avoid established colonies (Fletcher, 1973).

The term "ectocrine" was coined by Lucas (1947) to describe excretory substances of aquatic organisms which may have biological effects on other marine organisms. A review on algal ectocrines is available (Sieburth, 1968), but nothing seems to be known concerning analogous lichen products.

On the other hand, patches of *Lichina pygmaea* may occur completely surrounded by barnacle colonies (Stephenson and Stephenson, 1972). This suggests that *L. pygmaea* is not inhibitive towards invertebrates, an opinion supported by the large population of arthropods and molluscs obtained from that lichen (Colman, 1939).

C. Physical and Climatic Effects

Aspect of substrate affects the distribution and size of lichen patches, and thus also the populations of their associated invertebrates. The effect may be a simple one: larger lichen patches, growing on preferred aspects, can be expected to support larger and more diversified animal populations. Andre (1975) found the abundance of the cryptostigmatid *Carabodes labyrinthicus* on Belgian trees to be determined by corticolous lichen abundance, whereas the related *Dometorina plantivaga* appeared to prefer the lichens' southern colonies. The specific effect of aspect on certain groups of invertebrates may be more complicated. *Parmelia centrifuga* on granite rocks with a southern aspect maintained larger populations of prostigmatids, springtails and fly larvae than lichens on northern rocks, but the latter had more cryptostigmatids (Table VII; Stebaev, 1963). Tree face relative to compass-bearing did not appear to have any effect on tardigrade populations living in lichen colonies on Iowan trees. Tree height, however, affected the populations of one species, *Hypsibius tuberculatus*, which was most abundant at about 2 m above ground level. The populations of the four other tardigrades obtained were densest at ground level, decreasing with increasing lichen colony height on the trees (Kimmel and Meglitsch, 1969).

Data on the relative abundance of lichen-feeding psocids on larch trees with increasing altitude in Yorkshire were provided by Broadhead (1958). Turner and Broadhead (1974), working on the diversity and distribution of psocids on mango trees in Jamaica, showed that microepiphyte diversity (fungi, lichens and algae) based on percentage cover alone shows no relationship with either altitude or psocid diversity. However, epiphyte diversity calculated from epiphyte volume data increases significantly with increasing altitude and is significantly correlated with psocid diversity. Both the number of psocid species and their relative abundance appear therefore to be responding to changes in the complexity of their microhabitat which in turn are likely to be the product of changes in the climatic conditions prevailing at these various altitudes.

VIII. Discussion

A. Evolutionary Aspects

The prolonged association between lichens and invertebrates has had some evolutionary effects on these two groups of organisms. It is convenient to sum these aspects up under three headings: (1) concomitant evolution, (2) invertebrate adaptations to lichens, and (3) invertebrate effect on lichens.

1. Concomitant Evolution (in Sections II and III)

Many animals have been noted which have developed or were selected for extreme resistance to desiccation. This is also a lichen attribute. Components of the aquafauna are disseminated by winds—another lichen quality. At times a lichen propagule is blown about and settles while its protozoan, tardigradan or nematodan associate adheres to it. Thus it may be said that lichens and many members of its fauna were selected for the same characters, namely wind dispersal and the ability to withstand prolonged, intermittent periods of wetting and drying.

2. Invertebrate Adaptations to Lichens

The theory of lichen finding by invertebrates, whether for food or shelter, presumes that the animals have adapted their "life style" to life in and with lichens. The many mechanisms developed by arthropods to camouflage themselves with lichens and to mimic these cryptogams are all adaptations intended to exploit the protective presence of lichens. The recent rise to dominance of melanic forms of moths and psocids may be said to be an adaptation to the sudden disappearance of lichens.

The evolutionary effect of lichen diet on tineid moths (subfamily Meessiinae) was explored by Zagulyayev (1970). He stated that the transition in larval feeding habits from rotten wood and fungi to lichens must have necessitated a reorganization of the whole digestive system. The caterpillars also had to change their mode of life to carrying (and pupating in) cases which imitate their lichen substrate.

3. *Invertebrate Effect on Lichens*

Some authors (as summed up by Smith, 1921) believed that lichens produce their specific substances in response to invertebrate grazing. Although many arthropods and molluscs do feed on lichens, and the specific products are probably only by-products of lichen metabolism, this theory should not be discredited. It could probably be modified in the context of the "secondary plant substances" theory of Fraenkel (1959) mentioned above.

Formation of characteristic lichen galls in response to invertebrate feeders (and fungal parasites) suggests that this association is already old enough for lichens to react to their pests by characteristic and consistent growth.

B. Suggested Lines of Approach for Future Enquiry

The foregoing sections provide, at best, a rather incomplete picture of lichen–invertebrate associations. The reason for this fragmentary panorama is a distressing lack of experimental data about most aspects. Some of the more important areas in which information is in demand are:

1. Feeding and sheltering specificity.
2. Effect of lichen products on invertebrate grazers: specificity, mode of action, tolerance and possible detoxification.
3. Enzymatic studies on lichen digestion.
4. Energy budgets of lichen feeders, with associated physiological data.
5. Effect on grazers of radionuclides, heavy metals and pesticides accumulating in lichens.
6. Lichen dispersal through invertebrate agencies.
7. Effect of the pollution-mediated disappearance of lichens on dependent invertebrates.
8. Virgin lands, including deserts, forests and Arctic tundra are increasingly coming under "domestication". There are many indigenous lichens in these habitats harbouring invertebrate faunas. Data on these associations and the changes they undergo are unavailable.
9. Lichens may constitute the only source of energy in extreme-climate regions, such as hot and cold deserts, and yet very little seems to be known regarding food-webs emanating from such lichens. The same may be said about tropical areas, where invertebrates enjoy lush lichen growth.

10. Marine lichens offer opportunities to study some of the above problems under aquatic conditions.

There is a note of urgency in these proposals. Raven *et al.* (1971) point out that pollution, on a world scale, is increasing so rapidly that organisms are already becoming extinct at a high rate. Lichens are among the fastest disappearing organisms, and unless they, with all their unique associations, can be studied in the near future, we run the risk of not studying many of them at all.

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